

THE SKULL OF *MESENOSAURUS ROMERI*, A SMALL VARANOPSEID
(SYNAPSIDA: EUPELYCOSAURIA) FROM THE UPPER PERMIAN OF
THE MEZEN RIVER BASIN, NORTHERN RUSSIA

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ABSTRACT

Restudy of *Mesenosaurus romeri*, based on new and previously described cranial materials from the Upper Permian of the Mezen River basin of northern Russia, confirms its assignment to the synapsid eupelycosaurian family Varanopseidae. Comparisons with other members of the family support a pattern of relationship that recognizes two clades: one is composed of *Mesenosaurus* and *Mycterosaurus* for which the subfamily designation Myctersaurinae is proposed, and the other includes the remaining well-known varanopseids *Elliotsmithia*, *Varanops*, *Varanodon*, and *Aerosaurus* for which the subfamily designation Varanodontinae is proposed. Among the late Paleozoic synapsids, Varanopseidae has the longest fossil record, extending from the end of the Carboniferous to well into the Late Permian, and the widest geographical distribution, including North America, South Africa, and Russia.

KEY WORDS: Varanopseidae (*Mesenosaurus*), Synapsida, Upper Permian, Mezen River Basin, Russia

INTRODUCTION

The Mezen River basin of northern Russia has extensive exposures of Upper Permian sediments along the edges of several rivers, especially the Peza and Kimja rivers, both affluents of the Mezen River. These sediments, although visited only sporadically by paleontologists and geologists, have produced the skeletal remains of a diverse assemblage of amniotes, including numerous enigmatic parareptiles, at least two therapsids, and most interestingly a small synapsid of varanopseid affinities, *Mesenosaurus romeri* Efremov (1938). *Mesenosaurus romeri* was originally described on the basis of a partial skull, but its assignment by Romer and Price (1940) to the synapsid family Varanopseidae was only tentative, owing to the incompleteness of the holotype and only known specimen. A few additional specimens of *M. romeri* were recovered in the 1950s, which led to its more recent restudy by Ivachnenko (1978). These new specimens, including a poorly preserved articulated skeleton, were the basis of Ivachnenko's argument that *Mesenosaurus* was the oldest known archosaur (Evans, 1988; Carroll, 1988). As part of a systematic program of collecting in this area, several new specimens have been recovered and prepared, allowing a reevaluation of the anatomy and phylogenetic relationships of this interesting Paleozoic amniote. This study reaffirms the assignment of *Mesenosaurus* to the synapsid family Varanopseidae.

Anatomical structures are identified by the following abbreviations: an, angular; bo, basioccipital; co, posterior coronoid; d, dentary; ec, ectopterygoid; ex, exoc-

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cipital; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; o, opisthotic; p, parietal; pal, palatine; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; pra, prearticular; prf, prefrontal; ps, parasphenoid; q, quadrate; qj, quadratojugal; sc, sclerotic element; so, supraoccipital; sp, splenial; sq, squamosal; st, supratemporal; su, surangular; t, tabular; v, vomer.

SYSTEMATIC PALEONTOLOGY

Class Amniota

Subclass Synapsida

Eupelycosauria Kemp, 1982

Family Varanopseidae Romer and Price, 1940

Mycterosaurinae, **new subfamily**

Definition.—Varanopseid synapsids more closely related to *Mycterosaurus* than to *Varanops*.

Diagnosis.—Small varanopseid synapsids characterized by greatly expanded dorsal lamina of maxilla that contacts the prefrontal, resulting in the anterior shortening of the lacrimal to a level less than half the distance from the orbit to the naris and the loss of a nasal-lacrimal contact; prefrontal with well-developed ventral orbital process that contacts the palatine; paroccipital process of opisthotic anteroposterally, rather than dorsoventrally, expanded oval in cross section; caniniform region located far forward and at a level immediately behind the external naris.

Mesenosaurus Efremov, 1938

Type species *Mesenosaurus romeri* Efremov, 1938

Revised Diagnosis.—Mycterosaurine eupelycosaur characterized by the following cranial features: 1) premaxilla slender and with mate forms a narrowly rectangular snout in dorsal and ventral views; 2) dorsal process of premaxilla long and forms anterior half of dorsal margin of external naris; 3) deep excavation of the lateral surface of the body of the premaxilla narrows the base of the dorsal process to produce an expanded narial shelf that extends nearly to the snout tip; 4) palatal process of premaxilla with unusually long median suture; 5) well-developed depression on the lateral surface of the nasal that extends posteriorly from the narial border to nearly the anterior end of the prefrontal; 6) slight lateral swelling of the maxilla at the level of the caniniform tooth; 7) short posterior process of the maxilla fails to reach the level of the postorbital bar; 8) first premaxillary tooth smaller than the second and third teeth; 9) single, median vomerine tooth row; 10) postorbital cheek region of skull unusually broad and low, with nearly vertical posterior margin; 11) posterior edge of transverse flange of the pterygoid is angled slightly anterolaterally from basal articulation; 12) stapes slender, short, and rodlike, with modestly developed footplate and distally expanded quadrate process.

Mesenosaurus romeri Efremov, 1938

Holotype.—PIN (Paleontological Institute, Russian Academy of Sciences, Moscow) 158/1, partial skull and nearly complete right mandible (Fig. 1).

Referred Specimens.—PIN 3586/8a, partial skull of large individual (Fig. 2); PIN 3706/11, 3706/15, partial skulls of juvenile individuals (Fig. 3, 4), SGU (Saratov Geological Institute, Russia) 104 V/1558, partial skull, similar in size to the holotype (Fig. 5).

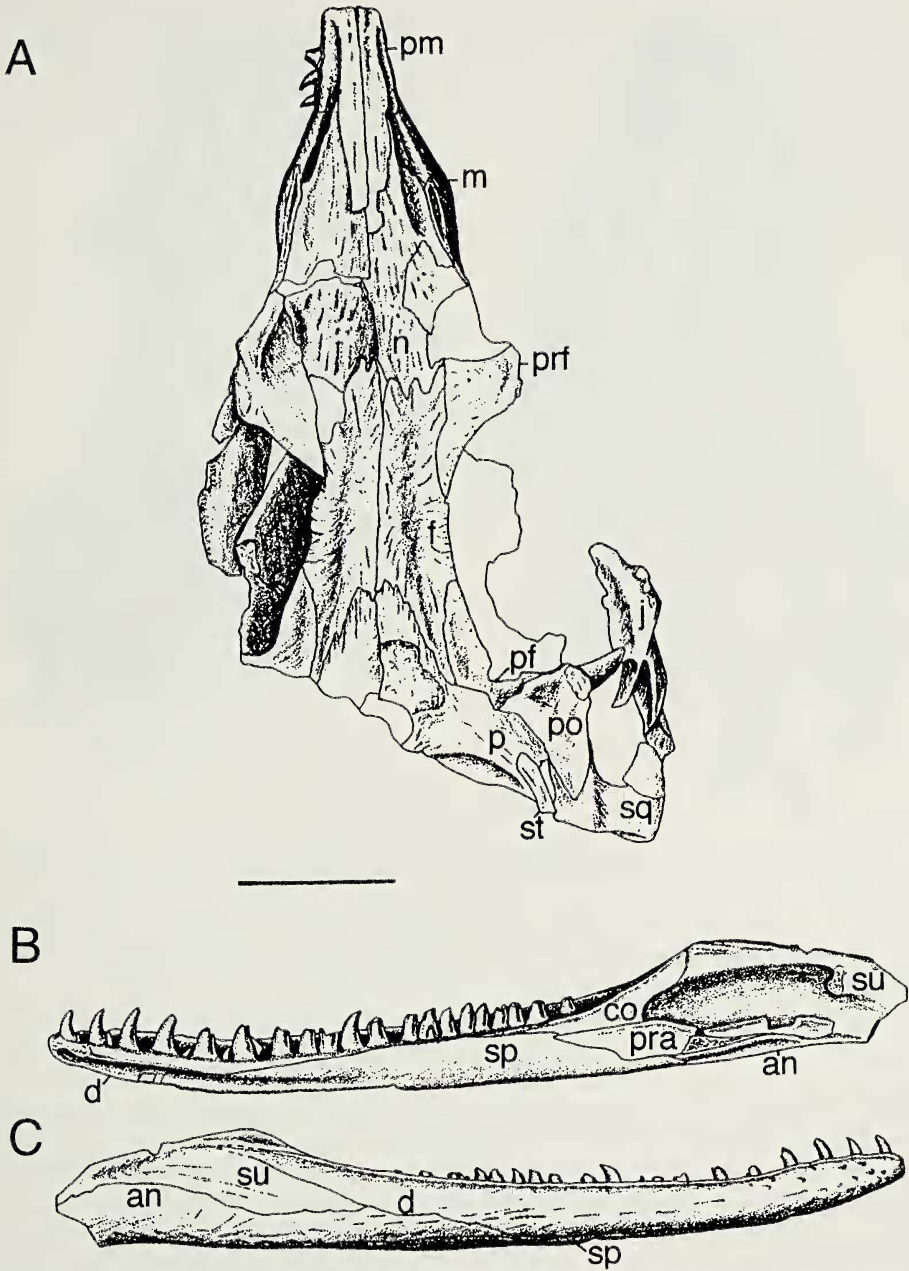


Fig. 1.—*Mesenosaurus romeri*, holotype PIN 158/1. A. Skull in dorsal view. B. Right mandible in medial view. C. Right mandible in lateral view. Scale = 1 cm.

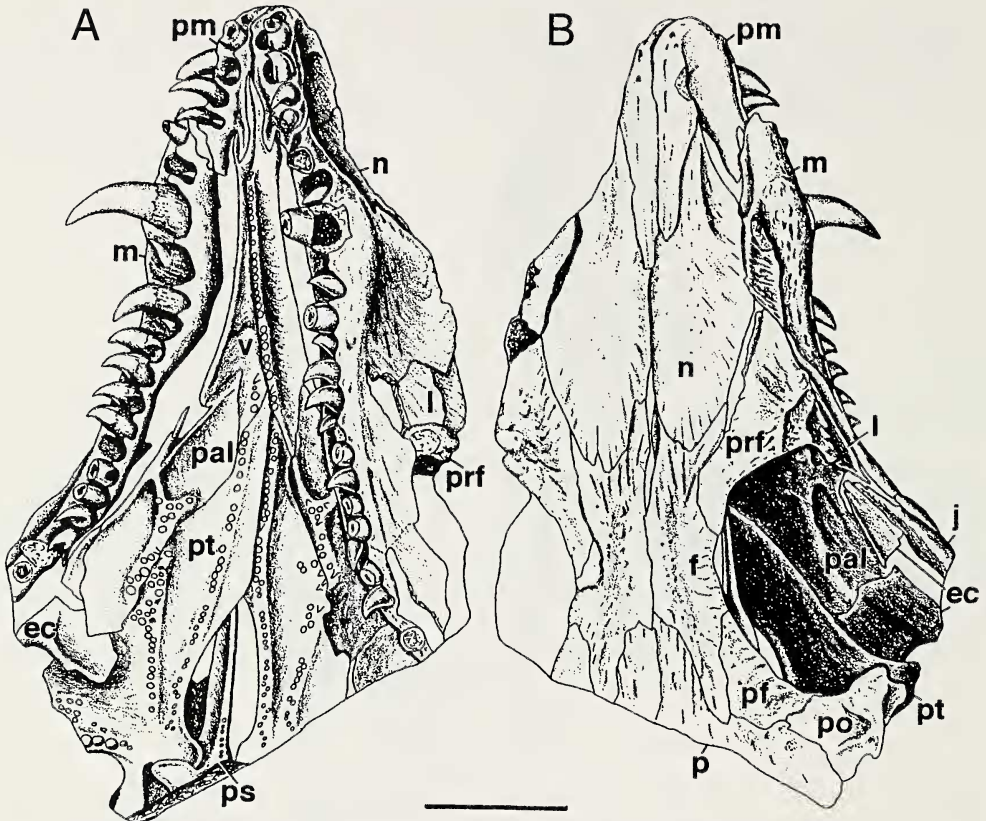


Fig. 2.—*Mesenosaurus romeri*, PIN 3586/8a, anterior part of largest known skull in ventral and dorsal views. Scale = 1 cm.

Horizon and Locality.—Mezen River Basin, northern Russia, Lower Tatarian, Upper Permian.

Diagnosis.—Same as for genus.

DESCRIPTION AND COMPARISONS

Skull.—General. The reconstruction of the skull shown in Figure 6 is a composite based primarily on the holotype, relying on the referred specimens only when necessary. Details of the snout region were available only in the larger specimens, whereas the posterior portions of the palate and braincase were well preserved only in the smaller, juvenile specimens. The pattern of the dentition was based largely on more mature specimens. As discussed below in the Discussion section, the Varanopseidae is recognized as being divisible into two subfamilies: the stem-based Mycterosaurinae is proposed for *Mycterosaurus* and *Mesenosaurus*, whereas all other known genera, *Elliotsmithia*, *Aerosaurus*, *Varanops*, and *Varanodon*, are included in the proposed stem-based Varanodontinae. With reference to this subdivision, the following description not only compares *Mesenosaurus* with *Mycterosaurus*, but also emphasizes features defining Varanodontinae as including taxa which are more closely related to *Varanodon* than to *Mycterosaurus*.

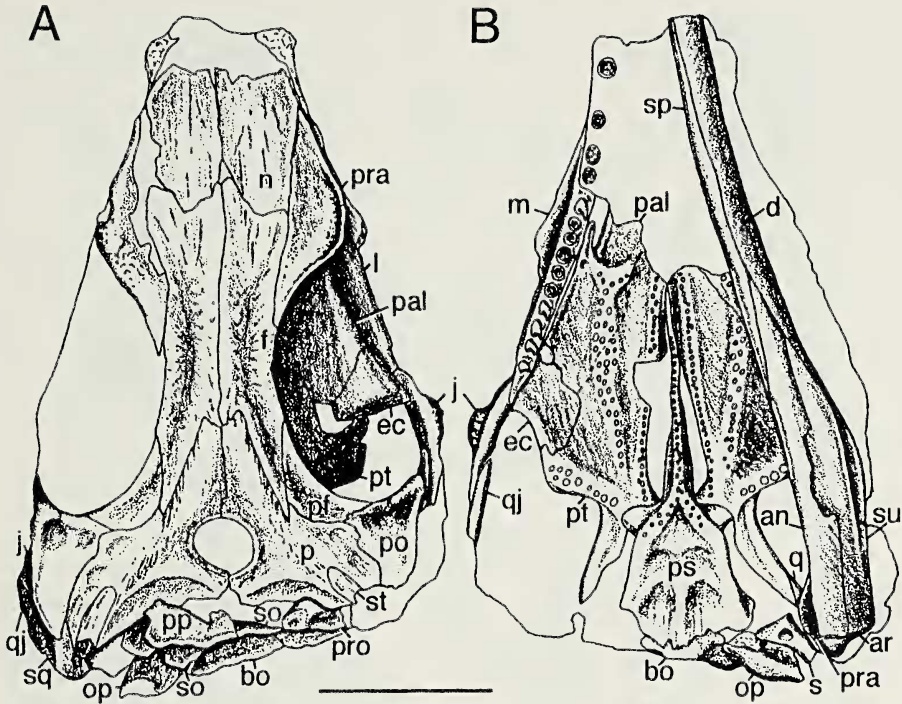


Fig. 3.—*Mesenosaurus romeri*, PIN 3706/11, nearly complete skull of juvenile in dorsal, and ventral views. Scale = 1cm.

In profile the skull has a low, subrectangular outline, with the occipital margin being normal to the jaw line. The skull outline is very distinctive in dorsal view, with the cheek regions diverging widely to about the level of the postorbital bar, where a sharply defined angulation then orients the temporal margins parallel to the midline. The snout of *Mesenosaurus* is unique among Paleozoic amniotes in being formed essentially by only the premaxilla and having a narrowly rectangular outline with a truncated tip in dorsal view. The orbit is unusually large and appears anteroposteriorly elongate because of the reduced height of the skull. The dorsal rim of the orbit is expanded slightly above the skull table as a rounded ridge. The parapineal foramen is large and located close to the posterior border of the skull roof. The lateral temporal fenestra is tall, occupying nearly the entire height of the skull. A pronounced sculpturing, consisting of a distinct pattern of grooves, covers most of the skull roof. In addition, a well-developed tubercular or nodularlike ornamentation extends along the orbital margins of the prefrontal, postorbital, and jugal. The internal nares are greatly elongated, equaling one-half the length between the snout tip and the anterior margin of the subtemporal fossa, and the palatal surface bears a complex pattern of tooth-bearing ridges. The unusually slender proportions of the lower jaw match those in other varanopseids.

Skull Roof.—The premaxilla, present in the holotype (Fig. 1) and PIN 4586/8 (Fig. 2), is large and possesses a minimum of five marginal teeth. In both dorsal or ventral views the paired premaxillae form a narrow, abruptly truncated snout tip with nearly parallel lateral margins, giving it a rectangular outline. Just above

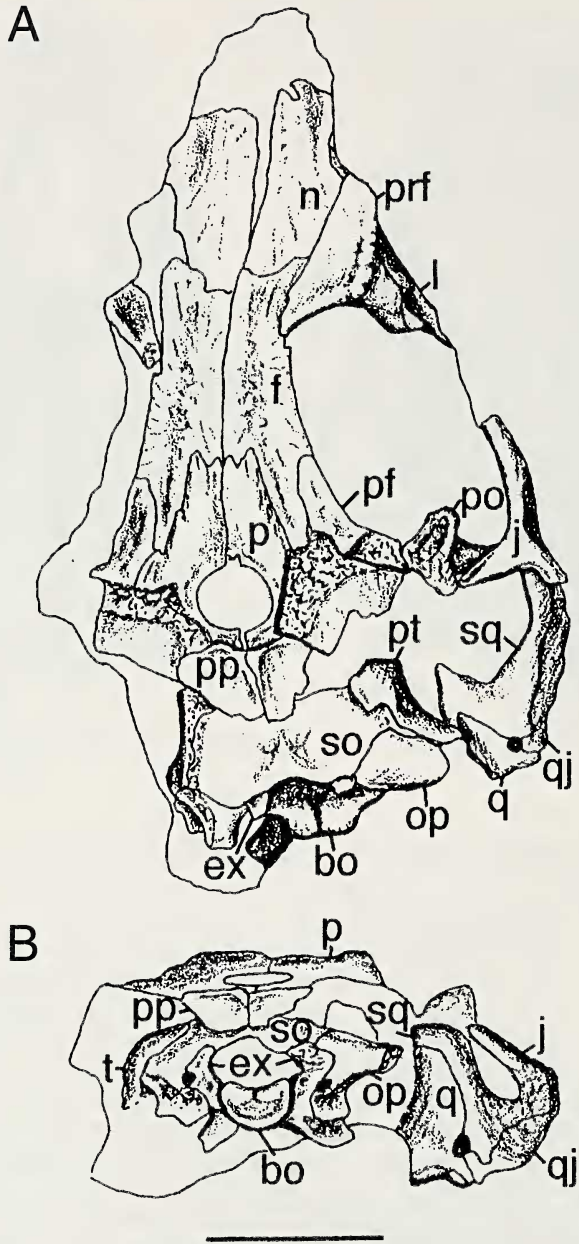


Fig. 4.—*Mesenosaurus romeri*, PIN 3706/15, partial skull in dorsal and occipital views. Scale = 1cm.

the marginal tooth row the lateral surface of the body of the premaxilla is deeply excavated so as to produce an expanded narial shelf that extends nearly to the tip of the snout. The excavation results in a narrowing of the base of the dorsal process, which is otherwise well developed in both length and width. The processes contact one another throughout their length, expanding slightly as they form the anterior half of the dorsal margin of the greatly elongated external nares,

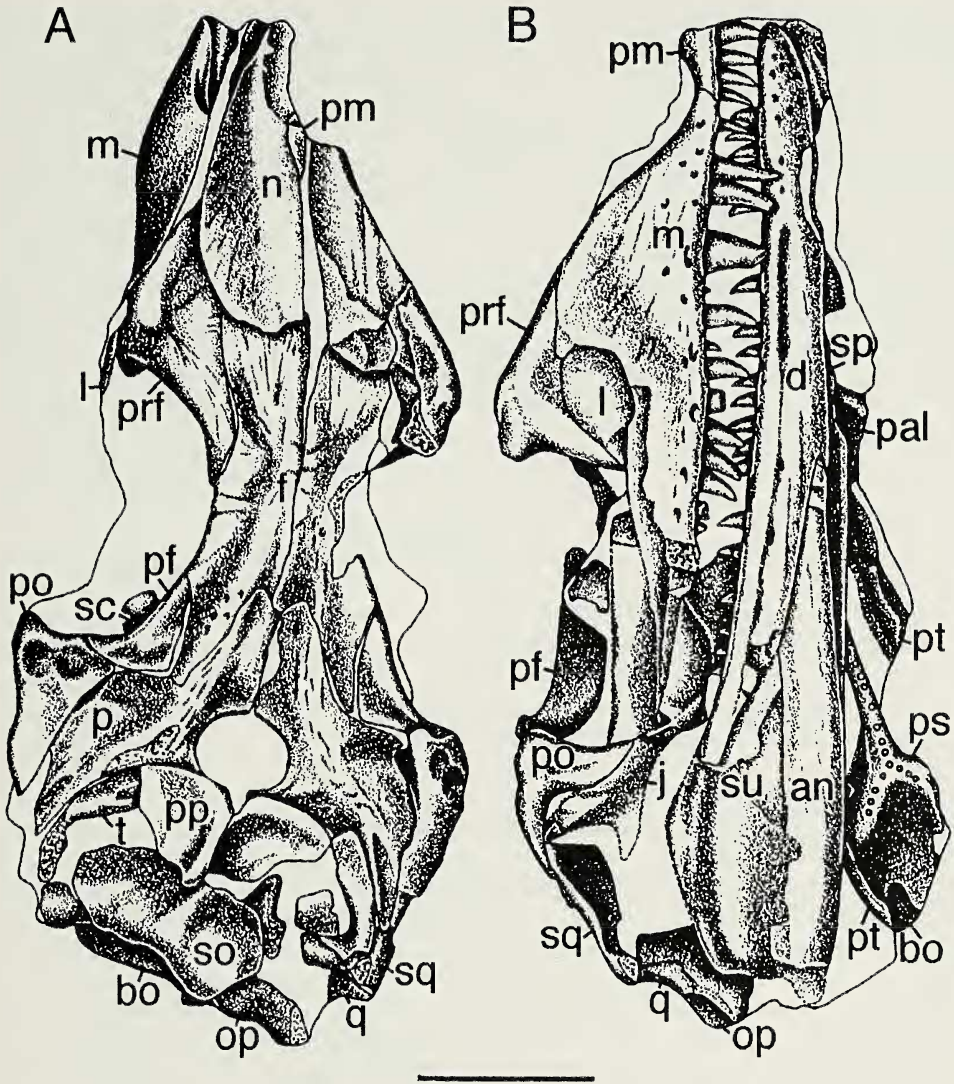
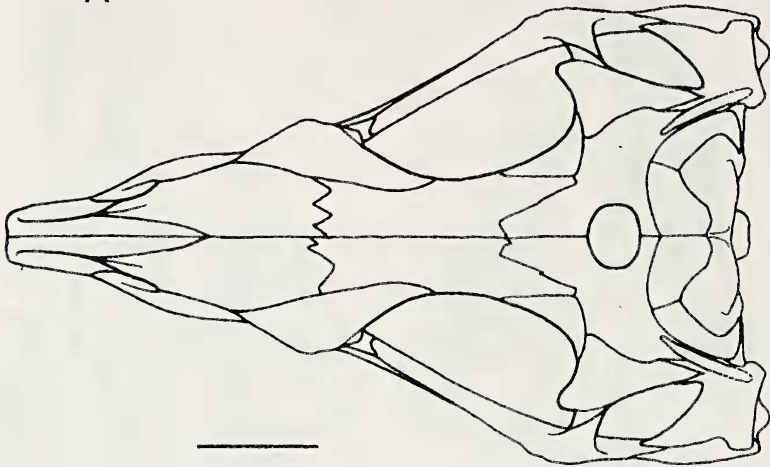


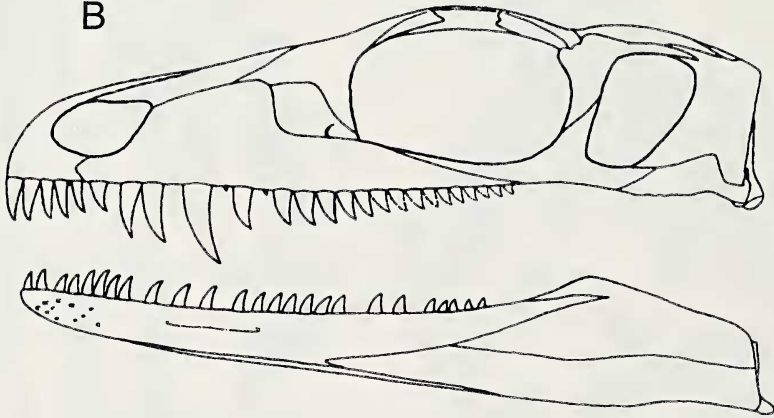
Fig. 5.—*Mesenosaurus romeri*, SGU 104V/1558, nearly complete skull with right mandible in dorsal and lateral views. Scale = 1 cm.

then narrowing as they extend between the nasals to a level well beyond the posterior borders of the external nares. The premaxilla forms nearly the entire ventral margin of the external naris. In contrast to all other late Paleozoic amniotes, there is no sharp, angular union between the dorsal and lateral surfaces of its subnarial bar, but rather, as seen only in varanopseids, the external surface of the subnarial bar is broadly rounded in transverse section. As on the skull roof, the extraordinarily narrow snout appears to be responsible for the extensive palatal contact between the premaxillae. Here their midline union extends over half the anterior, palatal length of the bone. Their remaining, posterior portions form a short palatal process which are narrowly separated along the midline by anterior

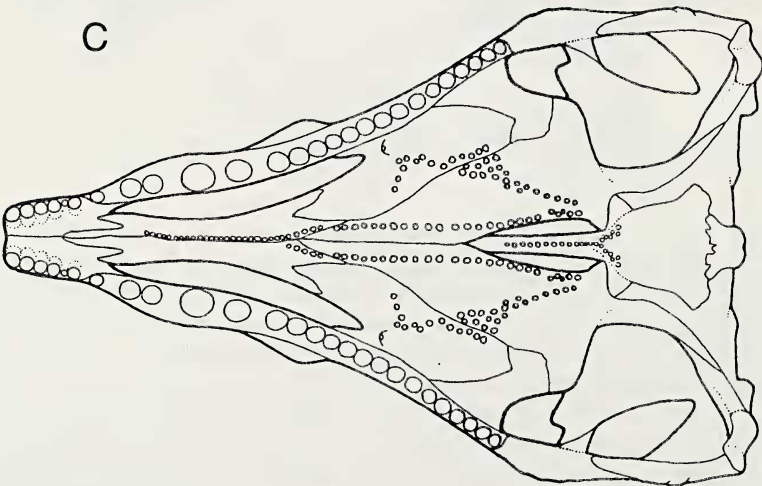
A



B



C



processes of the vomers before extending onto the ventral surface of the vomers. The premaxillary contribution to the internal naris is restricted to a very small portion of the anterior lateral border. A maximum of five teeth is borne by the premaxilla: the first is smaller than the second and third, but larger than the last two. The teeth are similar to those in other varanopseids in being closely spaced, strongly recurved, sharply pointed, and flattened from side to side with the larger teeth possessing a well-developed cutting edge along the distal half of the posterior edge.

The nasal exhibits a unique, well-developed depression that extends posteriorly from its anterolateral margin bordering the external naris to nearly the anterior end of the prefrontal (Fig. 2B). The width of the nasal in this region is narrowed greatly by the dorsal process of the premaxilla. A wide abutment, rather than the typical overlapping suture, marks the contact between the nasal and the dorsal lamina of the maxilla. The lateral margin of the broader, posterior half of the nasal is gently bowed ventrally to its contact with the maxilla and prefrontal. The frontal, preserved in all the specimens, exceeds slightly the nasal as the longest bone of the midline series, and its anterior process exceeds greatly the posterior process in width. As in other varanopseids, the contribution of the frontal to the orbital margin is extensive and is achieved by a medial emargination at the orbits, rather than by a lateral extension or lappet of the frontal as in sphenacodontids. The posterior process of the frontal is like that in *Mycterosaurus* in forming a narrow, triangular extension that diverges from the midline as it contacts the medial margin of the postfrontal. The broad parietals not only occupy most of the postorbital skull table (Fig. 3, 5), but also form a broadly triangular, anterior, midline process that extends well into the supraorbital region. The occipital margin of the parietal is broadly concave, with the posterolateral corner being drawn out into a winglike process. A well-developed occipital flange of the parietal is overlapped externally by the postparietal and tabular and therefore is not visible in the articulated skull. A deep, narrow groove on the posterolateral wing of the parietal received the anterior portion of the supratemporal; a distal portion of the supratemporal, not represented in any of the specimens, is presumed to have overlapped the squamosal. A short, narrow strip of the parietal posterolateral wing is exposed dorsally between the supratemporal and postorbital and is bordered distally by the squamosal. The unusually large, transversely oval parpineal foramen lies close to the posterior margin of the skull table. The large, roughly rectangular postparietals are restricted entirely to the occiput, have a deeply concave occipital surface, and unite in a median occipital ridge (Fig. 5). The median ridge ends just short of the ventral margin of the postparietals, below which each possesses a small, distinct, ventral medial process. Reexamination of the holotypic skull of *Mycterosaurus* reveals clearly the presence of paired postparietals and the same small process that defines the ventral limit of the median ridge.

In lateral view the ventral margin of the premaxilla and anterior half of the maxilla describe a straight, horizontal line, whereas more posteriorly there is a very slight dorsalward angulation (Fig. 5). The maxilla is long, extending to nearly the level of the postorbital, and widely separated from the quadratojugal by the

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Fig. 6.—Reconstruction of *Mesenosaurus romeri*. Skull in dorsal, lateral with mandible, and palatal views. Teeth shown as basal cross section. Scale = 1 cm.

jugal on the ventral margin of the skull. This is strongly contrasted by the pattern seen in all other known varanopseids, including *Mycterosaurus*, where the maxilla extends nearly to the level of the midlength of the subtemporal bar to contact the quadratojugal and exclude the jugal from the ventral margin of the skull. As in *Mycterosaurus*, however, the dorsal lamina of the maxilla is greatly expanded above the caniniform region to occupy a broadly rectangular area that not only excludes the lacrimal from the naris, but also shortens its length to a little over 40% of the distance between the orbit and the naris (Fig. 2, 5). In addition, the dorsal lamina is similar to that of *Mycterosaurus* and early therapsids in having a sufficient expansion to contact the prefrontal and prevent the lacrimal from contacting the nasal. The marginal dentition of the maxilla in the holotype PIN 158/1 includes 23 teeth and spaces. However, the posteriormost portion of the maxilla is incomplete, so the maximum number may have been slightly greater. The first tooth is nearly the length of the last premaxillary tooth but much smaller in basal diameter; the succeeding three teeth increase dramatically in size to a dominant caniniform tooth, and the postcaniniform teeth decrease steadily in size posteriorly. The general tooth morphology is identical to that of the premaxillary teeth. However, the well-preserved canines, as well as several postcanine teeth in PIN 3586/8a, exhibit very delicate serrations along the anterior and posterior cutting edges. It is likely that these serrations were present on all the teeth, but were lost during preparation. Confirming this, the mechanically prepared teeth of the right maxilla show no evidence of serrations, whereas those of the much more fragmentary left maxilla, which were exposed using nonmechanical methods, exhibit serrations. The serrations are so delicate and fine as to be not easily recognizable in other varanopseids. Contrary to the condition in *Mesenosaurus*, in all other varanopseids in which the maxillary dentition is known a caniniform region rather than a single, dominant caniniform tooth is exhibited. The state of this feature in *Elliotsmithia* is unknown due to the incompleteness of the holotype and only known skull (Dilkes and Reisz, 1996). The greatly reduced, subrectangular lacrimal makes only a narrow contribution to the anteroventral corner of the orbit (Fig. 5). As in *Mycterosaurus*, the lacrimal duct opens on the lateral surface of the skull near the orbital margin. Although poorly developed and not visible in lateral view, the suborbital process of the lacrimal contacts the jugal along the medial surface of the maxillary orbital margin.

The prefrontal, well preserved in all the specimens, is a large element with a broad, well-developed ventral, orbital process that nearly excludes the lacrimal from the orbit, then continues across the medial surface of the lacrimal to contact the dorsal surface of the palatine. As in other varanopseids, the prefrontal is divided longitudinally by an abrupt right-angled bend into distinct dorsal and lateral components. In *Mesenosaurus* the union between the two surfaces is accentuated by a strongly developed, tubercular or nodularlike ornamentation just anterior to the orbit. As a result, this area of the prefrontal extends outward to overhang slightly the lateral surface of the skull. Unfortunately, this area is not well preserved in *Mycterosaurus*. The small, subtriangular postfrontal is like that in *Mycterosaurus* in being restricted almost entirely to the dorsal skull table. The postorbital is similar to the prefrontal in being divided into distinct dorsal and lateral components (Fig. 1, 3, 5). This division is also accentuated by prominent tubercular or nodularlike ornamentation at the posterodorsal corner of the orbit, as well as by a depression on the dorsal surface. Although damaged, the postorbital in *Mycterosaurus* also exhibits all of the above features. In *Mesenosaurus*,

however, the ornamentation is so pronounced that the orbital rim of the postfrontal protrudes into the orbit. Despite the posterior process of the postorbital being long and broad, it is separated from the supratemporal by the parietal and squamosal.

As in all other varanopseids, the jugal is triradiate with slender, splintlike processes that form the ventral borders of the orbit and temporal fenestra, and the ventral half of the postorbital bar (Fig. 3, 4). Its anterior contact with the lacrimal is narrow and, as it occurs on the medial surface of the maxilla, is visible only in dorsal aspect of the skull. In strong contrast to the condition in other varanopseids, including *Mycterosaurus*, the jugal contributes to the ventral margin of the skull. This appears to be the result of the maxilla in *Mesenosaurus* not having the extraordinarily long posterior extension so characteristic of other varanopseids, and therefore, failing to contact the quadratojugal. A distinctive feature of the jugal is the presence of tubercular or nodularlike ornamentation at the posteroventral corner of the orbit. It is likely that similar ornamentation was also present in *Mycterosaurus*, but damage and/or poor preservation prevents confirmation.

The quadratojugal is a small element that contacts the jugal anteriorly and is overlapped slightly along its dorsal margin by the squamosal (Fig. 4). Posteriorly the quadratojugal exhibits an abrupt constriction along its dorsal margin as it wraps medially a short distance across the posterior surface of the squamosal. The quadratojugal then expands again to approximately its original height as it continues a short distance farther onto the posterior surface of the quadrate to interpose between the ventral margin of the quadrate foramen and the dorsal margin of the quadrate condyle. As in *Mycterosaurus* and *Elliotsmithia*, but in strong contrast to *Varanops*, *Aerosaurus*, and *Varanodon*, the quadratojugal is excluded from the ventral margin of the lateral temporal fenestra by an angular, anteroventral extension of the squamosal. The squamosal is roughly rectangular, but with its anterior margin deeply emarginated by the temporal fenestra (Fig. 1), creating anterior extensions of the squamosal above and below the fenestra that contact the postorbital and jugal, respectively. At the posterodorsal corner of the temporal region the squamosal curves slightly medially to make a narrow contribution to the dorsolateral corner of the occipital surface of the skull. Otherwise, the greater portion of the posterior margin of the squamosal is restricted to the lateral surface of the skull, rather than wrapping medially onto the posterior surface of the quadrate to form the occipital flange typically seen in early synapsids. This allows the posterior margin of the well-developed, bladelike dorsal process of the quadrate in *Mesenosaurus* to be visible in occipital view (Fig. 4). The dorsal process of the quadrate curves anteromedially as it contributes to the posterior, medial wall of the adductor chamber. Although most of the anterior margin of the dorsal process of the quadrate is not visible in any of the specimens studied, a conspicuous thickening defines its entire ventral margin, as it extends from the medial side of the condyle to contact the lateral surface of the posterior margin of the quadrate ramus of the pterygoid. A prominent quadratojugal foramen is located at the sutural intersection of the quadratojugal, squamosal, and quadrate. The condylar surface of the quadrate is not fully exposed in any of the specimens, but appears to be divided unequally into a smaller lateral and a larger medial condyle.

The supratemporal is rarely preserved in *Mesenosaurus*, and then is represented only by its anterior portion (Fig. 1, 3). As in other eupelycosaur, this element appears to be a slender strip of bone whose anterior portion is seated in a deep, narrow groove on the parietal. It was the empty anterior, parietal groove that was

misinterpreted as an upper temporal fenestra by Ivachnenko (1978). What appears to be a posterior portion of the groove for the supratemporal is faintly visible on the squamosal of PIN 3706/11 (Fig. 3). The tabular, preserved only in two specimens (Fig. 4, 5), is a narrow, somewhat sickle-shaped element whose convex anterodorsal margin conforms to the curvature of the occipital margin of the parietal with which it makes contact. Posteroventrally, however, the tabular ends in a small, distinct, posteromedially directed, hooklike process which appears to be present also in advanced varanopseids (Reisz, personal observation). The tabular is unknown in *Mycterosaurus*.

Palate.—Little is known about the palate of varanopseids, thus greatly restricting or even eliminating comparisons between that of *Mesenosaurus* (Fig. 6C) and other members of the family. The long, narrow internal nares are separated from one another by slender, elongate vomers (Fig. 2). For a short distance posterior to its extensive contact with the premaxilla, the vomer narrows slightly, then gradually expands to its sharply notched posterior end for the reception of the anterior end of the palatine. Beginning a short distance posterior to the premaxilla, the ventral surface of the vomer forms a deep, troughlike channel which parallels the midline closely. Possibly because of the narrowness of the snout, only one of the paired vomers bears a row of teeth on a prominent ridge that extends along most of their midline contact. At the point where the vomers diverge posteriorly from the midline, however, a second tooth row branches from the main, median row, and both angle slightly laterally for a short distance along the remaining medial margin of the vomers. Both rows of teeth are then continued directly posteriorly on the pterygoids. Although in the largest specimen, PIN 3596/8A, the vomer is paired throughout its length (Fig. 2), the condition in the partial holotypic skull PIN 158/1 (not figured) appears to be different. Here, only the anterior portions of the vomers are preserved, and they exhibit a midline suture separating only the paired, slender, vermiform anterior processes wedged between the posterior palatal processes of the premaxillae; the more posterior, internarial portions of the vomers are not suturally divided. The absence of the posterior, midline suture is especially evident in the short, edentulous region between the paired, anterior processes and the single, median tooth row, where only a weakly developed ridge is present. The palatine is a large element with extensive contacts with the pterygoid medially and the maxilla laterally (Fig. 2, 3). A deep, narrow notch on its anterior lateral margin forms the posterior corner of the internal naris, whereas its convex posterior margin incises deeply into the ectopterygoid. In contrast to most other synapsids, the palatine in *Mesenosaurus* is not a simple, sheetlike bone, but rather is distinguished by three prominent ventral ridges. Two of the ridges extend along its lateral and medial margins, with the former being much narrower and bordering the contact with the maxilla, whereas the latter is much wider and supports a field of small teeth. These two ridges are connected by a short, narrow, transverse ridge whose medial end also carries a few teeth. The ventral surface of the palatine is deeply concave between the ridges, particularly adjacent to the transverse ridge. Two foramina pierce the ventral surface of the palatine, one in the posteromedial angle formed by the lateral and transverse ridges and the other a short distance anterolaterally and adjacent to the palatine-maxillary suture.

In ventral view the ectopterygoid appears as a relatively simple, sheetlike bone that occupies a small, somewhat hourglass-shaped area. From a rather broad, lateral contact with the maxilla the ectopterygoid narrows to just beyond its mid-

length as it extends posteromedially, then expands again slightly before ending in a widely angular incisement in the anterolateral margin of the pterygoid just anterior to the transverse flange. The free, posterior edge of the ectopterygoid, forming the concave, anterior extension of the subtemporal fossa, has a smoothly rounded, ventral ridge. There are no teeth on the ectopterygoid. In dorsal view the ectopterygoid has a narrow anterior process, visible in PIN 3586/8 (Fig. 2), that not only covers the posterior half of the lateral margin of the palatine, but also contacts the medial surface of the jugal.

The pterygoid is the largest bone of the palate, forming most of the palatal surface (Fig. 2, 3). Three ridges bearing small teeth radiate across its ventral surface from a point near the basiptyergoid articulation. A single row extends immediately adjacent to the medial edge of the pterygoid and is smoothly continuous with the medial tooth row of the vomer. A second tooth row extends anterolaterally, beginning as a single row before expanding slightly into a narrow field which is smoothly continuous with that extending along the medial margin of the palatine. The posterior edge of the transverse flange supports a third row of about eight teeth. They are much larger than any of the other palatal teeth, although the last two or three teeth at either end of the series may decrease considerably in size. In addition, a series of smaller teeth is typically present immediately anterior to the lateral half of the principal tooth row. The palatal surface of the pterygoid between its toothed ridges is slightly concave. The lateral margins of the anterior or palatal rami of the pterygoids converge strongly toward the midline, where their sharply pointed ends wedge between the vomers. A short, narrow interptyergoid vacuity is partially closed posteriorly on either side of the midline by a stout, posteromedially projecting, triangular basal process of the pterygoid. The transverse flange occupies the same plane as the palate proper and therefore does not project below the level of the ventral rim of the skull. The posterior edge of the transverse flange angles slightly anterolaterally from the level of the basiptyergoid articulation. In palatal view the proximal portion of the quadrate ramus of the pterygoid extends posteriorly, whereas distally it curves slightly laterally. Its thickened ventral edge is smoothly rounded. It is not possible to make any useful comparisons with the palate of *Mycterosaurus*, as only the dorsal surface of its pterygoid is preserved, and then only as an impression (Berman and Reisz, 1982).

Braincase.—The fused parasphenoid and basisphenoid, the basiparasphenoid complex, is well preserved in PIN 3706/11 (Fig. 3), but only the parasphenoid component, which covers most of the ventral surface of the braincase, is visible. The narrow, long cultriform process is V-shaped in cross section. Its proximal portion, which divides the interptyergoid vacuity, supports a single row of small teeth, indicating that it occupied a level closely approximating the palatal plane. The precise extent of the distal edentulous portion, which would have extended dorsal to the pterygoids, is unknown. The laterally projecting basiptyergoid processes have the form of stout, subtriangular plugs. An articular facet on the anterior surface abuts against the posterior surface of the basal process of the pterygoid. As in other varanopseids, at the level of the basiptyergoid process the parasphenoidal plate expands abruptly posteriorly to about two-thirds its maximum width, then gradually expands to its posterior extent. In a manner identical to that in *Mycterosaurus*, the lateral margins of the parasphenoidal plate form prominent, ventrally expanded, rounded ridges which broaden slightly as they extend posteriorly to form the basisphenoidal tubera. In both forms the tubera

merge smoothly with the ventral keel of the cultriform process and each supports proximally a row of teeth like those on the keel. Between the tubera the parasphenoidal plate is deeply excavated, with the excavation deepening slightly on either side of a low, narrow, median ridge. The parasphenoid ends posteriorly in a feathered edge that ventrally overlaps the basioccipital.

A complete basioccipital-exoccipital complex with a well-preserved occipital condyle is present only in PIN 3706/15 (Fig. 4). As in other eupelycosaur, the condyle is roughly heart shaped, with the exoccipitals forming the dorsolateral corners of the condyle. They therefore also form the ventral and lateral margins of the foramen magnum, whereas this opening is bounded by the supraoccipital dorsally. As in *Mycterosaurus*, the supraoccipital is basically broad and flat, with only a slight median ridge. In contrast to the condition seen in larger varanopseids (Langston and Reisz, 1981), however, the dorsolateral process of the supraoccipital, usually extending above the posttemporal fenestra, is poorly developed. Although this area is incompletely preserved in *Mycterosaurus*, enough of the supraoccipital exists to indicate a similar configuration to that in *Mesenosaurus*. As in other synapsids, the opisthotic has a well-developed ventromedial process that not only contacts the lateral surface of the exoccipital, but also abuts ventrally against the basioccipital-parasphenoid complex. The morphology of the paroccipital process of the opisthotic also appears to be similar in *Mycterosaurus* and *Mesenosaurus*. In strong contrast to the condition seen in the larger varanopseids (Langston and Reisz, 1981), the paroccipital process is not dorsoventrally expanded and bladelike, but rather is nearly rodlike, with a slightly anteroposteriorly expanded oval outline in cross section.

The stapes, preserved in place in PIN 3706/11 (Fig. 3), exhibits a morphology that is strikingly different from those of other Permo-Carboniferous synapsids. It is a relatively slender, short, rodlike element except for a modestly developed, proximal footplate and distally expanded quadrate process. Adjacent to the footplate a large stapedia foramen pierces the shaft anteroposteriorly. A small rudiment of the dorsal process projects from the base of the footplate. The stapes resembles more closely those in early therapsids contemporaneous with *Mesenosaurus*, than those in the Permo-Carboniferous eupelycosaur. For example, the stapes in *Mycterosaurus* retains a large, massive footplate, a narrow neck between the footplate and a massive shaft, and a large dorsal process distal to the neck (Berman and Reisz, 1982).

Mandible.—The lower jaw is very elongate and slender, matching the proportions of the skull (Fig. 1, 6). In lateral view the tooth-bearing margin is only very slightly concave, and the coronoid eminence is very low, rising only slightly above the dentition. The ventral margin is nearly straight and only very slightly convex. The dentary, exposed principally in lateral view, occupies 80% of the mandibular length and from about its midlength tapers very gradually anteriorly to an extremely small symphysis that is confined almost entirely to an anterolaterally beveled surface at the end of the alveolar shelf. Posteriorly the dentary tapers to a long, acuminate process that lies in a groove on the lateral surface of the coronoid eminence of the surangular. The lightly built alveolar shelf has a maximum of 32 tooth positions. All the teeth are strongly recurved, sharply pointed, have slightly serrated anterior cutting edges, and exhibit only modest variation in size. They appear to increase in length slightly to about the fifth or sixth tooth, then gradually decrease to the posterior end of the series, with the last six teeth being considerably smaller than the anteriormost teeth. In lateral view of the jaw

the splenial has a very splintlike exposure along the central portion of the ventral margin, with its dorsal margin contacting nearly equal lengths of the dentary and angular. The splenial is the dominant element on the medial surface of the jaw. Its dorsal margin, sheathing the lateral surface of the central portion of the alveolar shelf, gradually tapers anteriorly to the ventral margin of the jaw, to end as a slender, splintlike process at the level of the third tooth position and well short of the symphysis. The angular is exposed as a large, elongate element, occupying the posterior, ventral half of the lateral surface of the jaw. Posteriorly it contacts the ventral margin of the surangular, whereas anteriorly it sharply wedges between the dorsal dentary and the ventral splenial. From its lateral exposure the angular wraps around the ventral margin of the jaw to a narrow, medial exposure below the posterior portion of the prearticular. As in other varanopseids, there is no development of a ventral keel of the angular; but rather it has a rounded ventral margin that is smoothly continuous with the curvature of the rest of the jaw (Fig. 3). All but a small anterior portion of the lateral wall of the adductor fossa is formed by the surangular, the thickened, dorsal margin of which rises gradually anteriorly into a low, angular, coronoid eminence.

The posterior coronoid is visible only in medial view of the jaw. Posteriorly it forms a short, narrow strip bordering the anterodorsal margin of the adductor fossa as it overlaps the medial surface of the surangular. Anteriorly the posterior coronoid narrows to a thin splint of bone which sheaths the posterior end of the medial surface of the alveolar shelf. There is no evidence of an anterior coronoid, and, although this is unusual among Permo-Carboniferous synapsids, the absence may be related to the unusually slender proportions of the mandible. Unfortunately, the mandible of *Mycterosaurus* is too poorly preserved in this area to allow comparison. Only in the holotype PIN 158/1 is the prearticular visible (Fig. 1), but most of its posterior extent is either poorly preserved or lost. What remains indicates a narrow strip for most of its extent along the medial or ventral border of the adductor fossa, widening considerably anteriorly before wedging sharply between the posterior coronoid and the splenial. The articular is exposed only partially in PIN 3706/11 and indicates the presence of a modest retroarticular process.

DISCUSSION

The Varanopseidae is a clade of small to medium-sized synapsids that can now be characterized by a relatively large number of autapomorphic skeletal features which are associated usually with highly predaceous, lightly built faunivores (Dilkes and Reisz, 1996; Reisz et al., 1998; and below). The family was erected by Romer and Price (1940) and originally contained two taxa, *Varanops brevirostris* and *Aerosaurus greenleorum*, which were collected from single, geographically and stratigraphically widely separated sites: the former from the well-known Early Permian (middle Leonardian) *Cacops* bonebed in the lowermost level of the undivided Clear Fork Group of Hentz (1988; revised from Arroyo Formation, Clear Fork Group, of Romer, 1974), Baylor County, north-central Texas, and the latter from the Late Pennsylvanian (Late Gzelian) Cutler/Abo Formation in El Cobre Canyon, Rio Arriba County, north-central New Mexico. Subsequent work has increased dramatically the list of known varanopseids to include *Aerosaurus welllesi* (Langston and Reisz, 1981) from the Early Permian (Wolfcampian) Cutler/Abo Formation, Arroyo de Agua, Rio Arriba County, New Mexico, *Mycterosaurus*

longiceps (Williston, 1915; Berman and Reisz, 1982) from the Early Permian (early Leonardian) Waggoner Ranch of the Wichita Group of Hentz (1988; revised from Clyde Formation, Wichita Group, of Romer, 1974), Mitchell Creek, Baylor County, Texas, *Varanodon agilis* (Olson, 1965) from the Late Permian (Guadalupian) Chickasha Formation, Blaine County, Oklahoma, and *Elliotsmithia longiceps* (Broom, 1937; Dilkes and Reisz, 1996; Reisz et al., 1998) from the Late Permian *Tapinocephalus* Assemblage Zone, Abrahamskraal, Western Cape Province, South Africa. Several taxa have been placed tentatively in Varanopseidae (Reisz, 1986), including *Nitosaurus jacksonorum* Romer and Price (1940), *Mycterosaurus smithae* Lewis and Vaughn (1965), *Milosaurus mccordi* (DeMar, 1970), and *Ruthiromia elcobriensis* Eberth and Brinkman (1983).

The cranial anatomy of *Mesenosaurus* provides overwhelming evidence of its varanopseid affinities in possessing the following synapomorphies: 1) dorsoventral expanded temporal fenestra occupies most of the height of temporal region, resulting in narrow subtemporal bar (some caseids show a similar condition); 2) marginal dentition is composed of strongly recurved, laterally compressed, sharply pointed teeth with fore and aft cutting edges restricted to the distal half of the tooth; 3) well-developed premaxillary subnarial shelf whose external surface is broadly rounded in transverse section; 4) anterior median process of the parietal extends into the supraorbital region of the skull table; 5) small postfrontal is bordered medially by a narrow, posterior process of the frontal; 6) tabular is reduced to a small, narrow element that contacts the medial margin of the posterolateral wing of the parietal; 7) absence of a medial, occipital flange of the posterior margin of the squamosal that covers the posterior margin of quadrate; 8) parasphenoid plate is broad throughout its length and the basisphenoidal tubera are winglike and extend far laterally and posteriorly from the base of the cultriform process; and 9) a very prominent, nodular or tubercularlike ornamentation is present on the orbital margins of the prefrontal, postorbital, and jugal.

The ninth varanopseid character listed above deserves some explanation, as it is so strikingly pronounced in the well-preserved skulls of *Mesenosaurus* that Efremov (1938) originally considered it to be an autapomorphy of the genus. Careful examination, however, reveals the presence of this feature in other varanopseids in which the orbital bones are sufficiently preserved, despite in most instances severe damage due to over preparation. As examples, the holotypes of *Mycterosaurus longiceps* and *Varanops brevirostris* exhibit evidence of the same orbital-rim ornamentation found in *Mesenosaurus*. *Elliotsmithia* also exhibits the presence of this type of ornamentation on the same three orbital bones, although not commented on in the latest descriptions (Dilkes and Reisz, 1996; Reisz et al., 1998). Although the relevant regions of the prefrontal and postorbital in the holotype of *Aerosaurus wellesi* are too damaged to determine the presence of this feature, the well-preserved jugal exhibits the *Mesenosaurus*-like ornamentation. Therefore, it is likely that the unusual pattern of ornamentation so well exemplified in *Mesenosaurus* actually diagnoses all varanopseids recognized to date.

Mesenosaurus exhibits a number of cranial features recorded previously only in *Mycterosaurus*. Two of the most unusual of these are in the distinctive morphology of the maxilla, as they mimic the therapsid pattern in this structure: 1) the massive, anteroposteriorly broad dorsal lamina contacts the prefrontal, preventing contact between the nasal and lacrimal and reducing the lateral exposure of the lacrimal to a small, subrectangular area; and 2) the dorsal lamina forms a thick, deeply striated, abutment contact with the nasal. In both genera the pre-

frontal appears to be larger than in other varanopseids, with a well-developed ventral orbital process that nearly excludes the lacrimal from the orbital rim before continuing medially to it to contact the dorsal surface of the palatine. In both *Mesenosaurus* and *Mycterosaurus* the paroccipital process of the opisthotic is short and rodlike and, therefore, in sharp contrast to that in other varanopseids, where it is moderately to greatly expanded dorsoventrally into a bladelike structure. Outgroup comparison with caseosaurs and ophiacodonts indicates that the latter state may be primitive for the family, but this is not certain. Although there are no well-preserved postcranial skeletons of *Mesenosaurus* in the collections of the Paleontological Institute of the Russian Academy of Sciences, a privately owned specimen reveals a number of features which, as far as known, occur also only in *Mycterosaurus* among the varanopseids. These include the presence of a modest lateral excavation at the base of the neural arches, two subequally developed sacral vertebrae, and the absence of a supraglenoid foramen. Ongoing collecting from Mezen has already yielded new postcranial materials, preparation of which has just been initiated.

Mesenosaurus and *Mycterosaurus* possess a number of features which appear in the derived state in other varanopseids, the most striking of which occur in the temporal region. In *Elliotsmithia*, *Varanops*, *Aerosaurus*, and *Varanodon* the temporal fenestra is expanded posteroventrally, resulting in an unusually large, roughly triangular-shaped opening. Possibly associated with this feature is a strong anterodorsal inclination of the occipital surface of the skull so that the braincase and the closely associated quadrate and quadrate process of the pterygoid are uniquely positioned relatively far anteriorly to occupy a position well into the region medial to the temporal fenestra. A consequence of this change in skull proportions is the reduction of the adductor chamber, the space normally formed between the parietal and postorbital bones dorsally, the quadrate ramus of the pterygoid medially, the quadrate and squamosal posteriorly, and the zygomatic arch laterally. Two derived features of *Aerosaurus*, *Varanops*, and *Varanodon* which appear in the primitive state in *Mesenosaurus* and *Mycterosaurus* include the presence of a well-developed retroarticular process of the articular and the inclusion of the quadratojugal into the temporal fenestra. Unfortunately, in *Elliotsmithia* the posterior region of the mandible is not sufficiently preserved to indicate the presence or absence of a retroarticular process. The presence of a long posterior process of the jugal which contacts the squamosal to exclude the quadratojugal from the temporal fenestra in *Elliotsmithia*, as it does in *Mycterosaurus* and *Mesenosaurus*, is the one notable contradiction to the dichotomy of the varanopseids proposed here.

CONCLUSIONS

In the recent study of the varanopseid *Elliotsmithia longiceps* by Reisz et al. (1998) a cladistic analysis of the phylogenetic intrarelationships of the family was presented that demonstrated a basal dichotomy, and, although two distinct clades were recognized, subfamilial units were not formally proposed for either. The cladogram of Varanopseidae phylogeny presented by Reisz et al. (1998) is reproduced here (Fig. 7), as it agrees with the comparative, anatomical data presented above and therefore supports the following generic relationships and subfamilial assignments: 1) *Mesenosaurus* is a member of the family Varanopseidae as a sister taxon to *Mycterosaurus* and together they form a clade which is assigned here

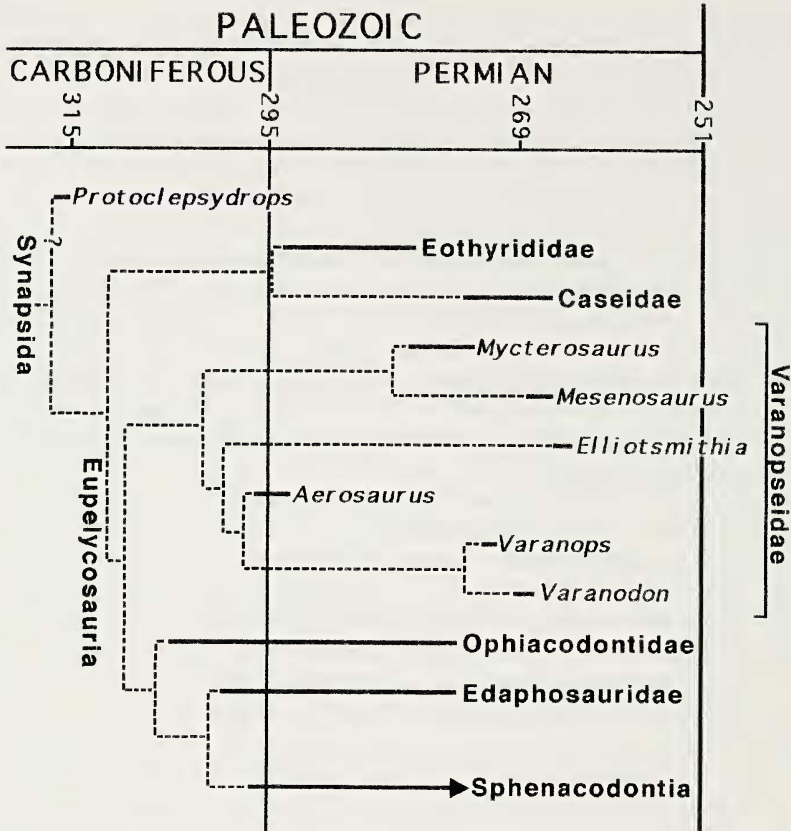


Fig. 7.—Cladogram showing relationships of varanopseids. Modified from Reisz et al. (1998).

the stem-based subfamily designation Mycterosaurinae; and 2) the remaining well-known genera *Elliotsmithia*, *Varanops*, *Varanodon*, and *Aerosaurus* form a sister clade. The stem-based subfamily designation Varanodontinae is assigned to the latter clade and can be diagnosed by the following autapomorphies which are noted here and in the recent studies by Dilkes and Reisz (1996) and Reisz et al. (1998): 1) anterodorsal process of the squamosal forms the dorsal border of the temporal fenestra; 2) posteroventral margin of temporal fenestra expanded, resulting in the opening having a broadly triangular outline and, with the exception of *Elliotsmithia*, incorporating the quadratojugal; 3) occipital surface of skull slopes anterodorsally at nearly 45°, resulting in a forward displacement of the braincase to the level of the temporal fenestra; and 4) presence of a well-developed retroarticular process (unknown in *Elliotsmithia*).

The presence of varanopseids not only in North America and South Africa (Dilkes and Reisz, 1996; Reisz et al., 1998), but also in Russia makes these small to medium-sized faunivores the most widely dispersed synapsids of their time. As in the case of the South African *Elliotsmithia*, the association of *Mesenosaurus* with a Late Permian faunal assemblage that includes parareptiles and basal therapsids provides indisputable evidence that the temporal range of basal eupelycosaurian varanopseids extended well beyond the Early Permian. In addition, their

fossil record is the longest of any group of Paleozoic synapsids, extending from the end of the Carboniferous to well into the Late Permian, a span of nearly 40 million years. This unusual longevity is coupled, however, with a very sparse fossil record (Reisz et al., 1998). Whereas other systematically equivalent groups of Permo-Carboniferous synapsids are represented by significantly larger numbers of specimens, varanopseids are known on the basis of only a few specimens, with most of the species being represented by specimens only from the type localities. Although *Aerosaurus* and *Mycterosaurus* are both recognized by two species restricted to their type localities (Lewis and Vaughn, 1965; Langston and Reisz, 1981; Berman and Reisz, 1982), *Varanops*, *Varanodon*, *Elliotsmithia*, and *Mesenosaurus* are all monotypic and limited to single localities, and of these *Varanodon* and *Elliotsmithia* are known from single specimens (Romer and Price, 1940; Olson, 1965). In the absence of adequate documentation, the rarity of varanopseid specimens can be interpreted in one of two ways: 1) reflecting their actual relative abundance as rare components of faunal assemblages, or 2) indicating an evolutionary radiation restricted to terrestrial environments which are rarely preserved in the fossil record and/or inadequately sampled.

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